

Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data

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ABSTRACT: Patterns of vertical movement in pelagic predators can be highly complex, reflecting behaviours such as foraging, thermoregulatory excursions and spawning. Here we used fast Fourier analysis to identify periodicity in the vertical movements of 6 basking sharks *Cetorhinus maximus* from archival tagging data that totalled 595 d. We analysed quantitatively fine-scale vertical movements of basking sharks over seasonal scales (May to February) and detected predominant periodicities related to the vertical movements of the sharks' zooplankton prey. Normal and reverse diel vertical migration (DVM) represented the main periodic dive behaviour, occurring for 11 to 72% of individual track times. A tidal pattern of vertical movement, previously unreported for sharks, was also identified. A possible mechanism for this behaviour appears related to the shark exploiting tidally-induced aggregations of zooplankton prey at depth. The youngest shark tagged showed a markedly different pattern of vertical behaviour. Long-term data sets of swimming depth are becoming increasingly available for pelagic predators from pressure-sensitive data loggers. This study demonstrates the utility of signal processing techniques in objectively identifying both expected and unexpected periodicity in these continuous, high-resolution tracks.

KEY WORDS: Telemetry · Fourier analysis · Dive profile · Strategy · Fish · Whale · Seal

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INTRODUCTION

Diel, tidal and lunar rhythms have been observed in the reproductive, locomotor, feeding and moulting behaviour of a range of marine organisms (e.g. Hays et al. 2001, Queiroga & Blanton 2005, Skov et al. 2005). For organisms at low trophic levels, there may be a strong advantage in coordinating activity with a certain phase of an abiotic cycle where it offers a reduction in predation pressure. For instance, zooplankton throughout the world's oceans are known to conduct a diel pattern of vertical migration (DVM); moving up in the water column at dusk and returning to depth at

dawn, in order to feed whilst minimising the risk of predation from visual predators (Hays et al. 2001). Planktonic organisms can also be passively influenced by the tidal cycle, being advected by tidal currents (Cotte & Simard 2005), aggregated in tidal fronts or concentrated against topographic features (Genin 2004).

Whilst higher pelagic predators are less likely to be directly affected by these cycles, they are known to respond to cyclical patterns in prey availability by adjusting patterns of activity and habitat selection accordingly (Croll et al. 1998, Baird et al. 2001). In this way the effect of diel, tidal and lunar cycles can propa-

gate up the food chain, leaving stereotyped signatures in patterns of predator movement (e.g. Wilson et al. 1993, Cartamil & Lowe 2004).

High-resolution data on the vertical movements of large marine organisms can be collected by attaching archival tags, which can record depth frequently and store data for up to many years (e.g. Arnold & Dewar 2001). However, the identification of rhythmical movement patterns in these data can be difficult because organisms' responses can change rapidly with respect to a changing environment, rhythms can be hard to detect when they exert an influence over monthly or seasonal cycles, and different signals may confound each other where they occur simultaneously.

Signal processing techniques such as fast Fourier analysis accurately summarise the relative importance of periodic components within time-series, and are well-suited to the analysis of archival tagging records as they achieve rapid throughput of high-resolution data (Graham et al. 2006). They also provide advantages over techniques such as autocorrelation, which are likely to require preliminary de-trending of the depth record (Neat et al. 2005). Summary swimming depth data in plankton-feeding basking sharks *Cetorhinus maximus* has shown that they do not hibernate but remain vertically active in the winter (Sims et al. 2003). DVM has also been identified subjectively in short, isolated portions of 4 archival tracks to date (Sims et al. 2005). However, fine-scale depth movements for *C. maximus* have yet to be analysed objectively at a seasonal scale. In this study, fast Fourier transforms were applied to swimming depth data for 6 basking sharks from archival tags. The aim was to identify periodic components in the dive records, in order to detect underlying influences on the complex dive behaviour of a non-air breathing vertebrate and examine how these changed across seasonal scales.

MATERIALS AND METHODS

Archival tagging. Basking sharks were tagged from May to July in 2001, 2002 and 2004 (Table 1) with pop-up archival transmitting (PAT) tags (PAT Versions 2, 3 and 4; Wildlife Computers) using methods given in Sims et al. (2003). Tagging procedures conformed to institutional and national ethical guidelines. PAT tags incorporated an Argos-certified transmitter with a data logger that recorded pressure to 1000 m, water temperature (−40 to 60°C) and light level ($W\ cm^{-2}$ at 550 nm wavelength) at 1 min intervals for the duration

of tag deployment. All tags were programmed with the same sampling attributes except the tag on Shark 1 which did not record depths greater than 160 m, however, only 1.26% of the total track time occurred below 160 m. All tags were pre-programmed to release from the shark after data recording periods of between 7 and 229 d (mean 103.8 d; Table 1). The full archival data set was only accessible upon recovery of the tags. Six tags were retrieved (Table 1) representing 24% of the total tags deployed to date ($n = 25$). Geolocations were calculated as described in Sims et al. (2003, 2006). Shark length and sex were recorded where possible at the time of tagging (Sims et al. 2003).

Dive analysis. The fast Fourier transform (FFT) operates by approximating a function with a sum of different sine and cosine terms (Chatfield 1996). The influence of each periodic component is indicated by the magnitude of the corresponding spectral peak in the periodogram. The FFT is particularly well-suited to analysing long-term, high-resolution data sets such as those from archival tagging studies as the resolution and range of detectable frequencies are directly related to the sampling frequency and duration (Graham et al. 2006). Specifically, fast Fourier transforms can identify periodicities up to the Nyquist frequency, which is half the sampling rate, and in this study was 1 cycle $30\ s^{-1}$ (Chatfield 1996). Furthermore, there is potential for extremely high spectral resolution, as the FFT-generated spectrum contains $N/2$ distinct frequency components and adjacent components are separated by Δf , defined as the sampling frequency/ N . These traits also differentiate the FFT from autocorrelation and periodogram analyses that produce outputs of lower spectral resolution.

Depth data were extracted from archival tag records and routinely corrected for pressure-sensor drift. An FFT was applied to the full depth record for each shark and monthly sub-sections of the tracks using programming routines in MATLAB (MathWorks)¹. Due to the

¹Programming codes available on request

Table 1. *Cetorhinus maximus*. A summary of the archival tags retrieved from the 25 deployed on basking sharks during May to July 2001, 2002 and 2004. Sex (F = female) is included where known. (j) the only shark known to be a juvenile; days: no. of track days. Dates given as d/mo/yr

Shark no.	Shark length (m)	Sex	Date tagged	Tag location °N	Tag location °W	'Pop-up' location °N	'Pop-up' location °W	Days
1	4.5	F	24/5/01	50.38	4.11	56.42	7.26	77
2	6.0		25/5/01	50.32	4.13	49.87	2.42	197
3	6.5		31/7/01	55.87	5.39	55.59	5.12	52
4	2.5(j)		31/7/01	55.89	5.40	51.67	6.64	229
5	6.0	F	18/6/02	50.18	4.26	50.35	5.17	7
6	4.5		01/6/04	50.26	4.03	50.93	4.59	33

finite, non-stationary nature of the data set, the FFT spectral components can interfere with each other, and generate frequency peaks that do not represent true periodicity in dive behaviour. A 'hamming' window function was therefore used to reduce the effect of adjacent spectral components (Oppenheim & Schaffer 1989) and aid identification of biologically meaningful spectral peaks. An FFT was also applied to sections of the track where a shark conducted a consistent pattern of dive behaviour, in order to check that the FFT identified known periodic movements such as DVM where the amplitude and rate of diel vertical migrations varied. In addition, tracks were visually scanned for periods of DVM, in order to score the percentage time that individual sharks conducted DVM per month. For this purpose DVM was defined as 2 consecutive crepuscular changes in average depth.

Activity rate. Programming routines in MATLAB were used to calculate vertical distance moved $\text{min}^{-1} \text{d}^{-1}$ by fitting a high-order polynomial to the dive tracks, using 15 points either side of each depth value¹. This estimated vertical distance moved without any mathematical approximation.

Tidal data. A spectral peak was identified with the same period as the tidal cycle in one shark (Shark 2). To characterise this shark's vertical movements in relation to the tidal phase, depth records were assigned to 'flood' and 'ebb' categories over a period of 10 d where this behaviour was clearly identifiable and compared using a Mann-Whitney test. Geolocations and the archival depth records indicated that at this time the shark was located in the deepest area within Hurd Deep, central western English Channel (49.50°N, 2.15°W). Times of high and low water were calculated using Polpred V.2 (Proudman Oceanographic Laboratory, Liverpool, UK). Swimming depths within 1 h of high and low water were excluded from the analysis to allow for variation in location. Times of high water varied by up to 1 h along Hurd Deep.

A frequency peak with a period of 13.8 d was observed in the periodogram for Shark 2. In order to corroborate whether this corresponded to the spring-neap tidal cycle a circular-linear correlation was performed between the vertical distance moved per day and the lunar phase for months where monthly spectra indicated a tidal influence. The circular-linear correlation was performed using Oriana V. 1.0 (Kovach). Daily values of lunar phase (as percentage of the moon visible) were obtained from a nautical almanac.

Zooplankton data. Data on copepod abundance were obtained from the continuous plankton recorder (CPR) survey as monthly values averaged from 1958 to 2002 for an area comprising the western English Channel extending out to the shelf edge. (See Richardson et al. [2006] for detailed CPR methodology.)

RESULTS

General features

All basking sharks tracked remained on the continental shelf to the west of the UK. At weekly to monthly scales the tracks were characterised by continuous movement through the water column and generally showed frequent returns to the surface (Fig. 1). In contrast, Shark 4 remained at one depth for periods of up to 2 wk. Shark 3 also remained at depth for 14 d in the first 2 wk of September. Dives were classified as 'yo-yo' dives when sharks moved from surface to depth repeatedly with little time at the top or bottom of each dive. Within yo-yo dives, the average rate of descent was significantly faster than the average rate of ascent for all sharks (Wilcoxon paired-sample test, $n = 20$ dives per shark), with the smallest difference in Shark 4 (Table 2).

Dive periodicity

Periodograms calculated for each shark all had large spectral peaks near zero. This was a consequence of the dive data being offset by the average dive depth, so only peaks following this initial slope represented periodic signals in the dive data. The main spectral peaks were found both with and without the 'hamming' window indicating they were not artefacts. The curtailing of depth readings to 160 m in the tag from Shark 1 could have caused a non-linear effect in the FFT and a merging of close frequency peaks in the periodogram. However, spectral components in this periodogram were distinct indicating no bias (Fig. 1). No frequency peaks were found to be associated with a yo-yo pattern of vertical movement. The periodogram from Shark 4 was different from those of the other sharks, having spectral peaks with periods of 17.3, 12.1 and 7.2 d, although these were of relatively small magnitude (Fig. 1). The main spectral peaks in other sharks were as follows.

Diel movements

Fast Fourier analysis revealed that the dominant periodicity in the vertical movements of Sharks 1, 3, 5 and 6 was 1 cycle d^{-1} (period range 20.3 to 24.1 h) (Fig. 1). This periodicity was also strong in Shark 2 but was not dominant. Control analyses confirmed that DVM was associated with a spectral peak at 1 cycle d^{-1} regardless of the amplitude, relative depth, or rate of vertical migration. In Sharks 3 and 6 there were second, smaller spectral peaks at exactly 2 cycles d^{-1} ,

¹Programming codes available on request

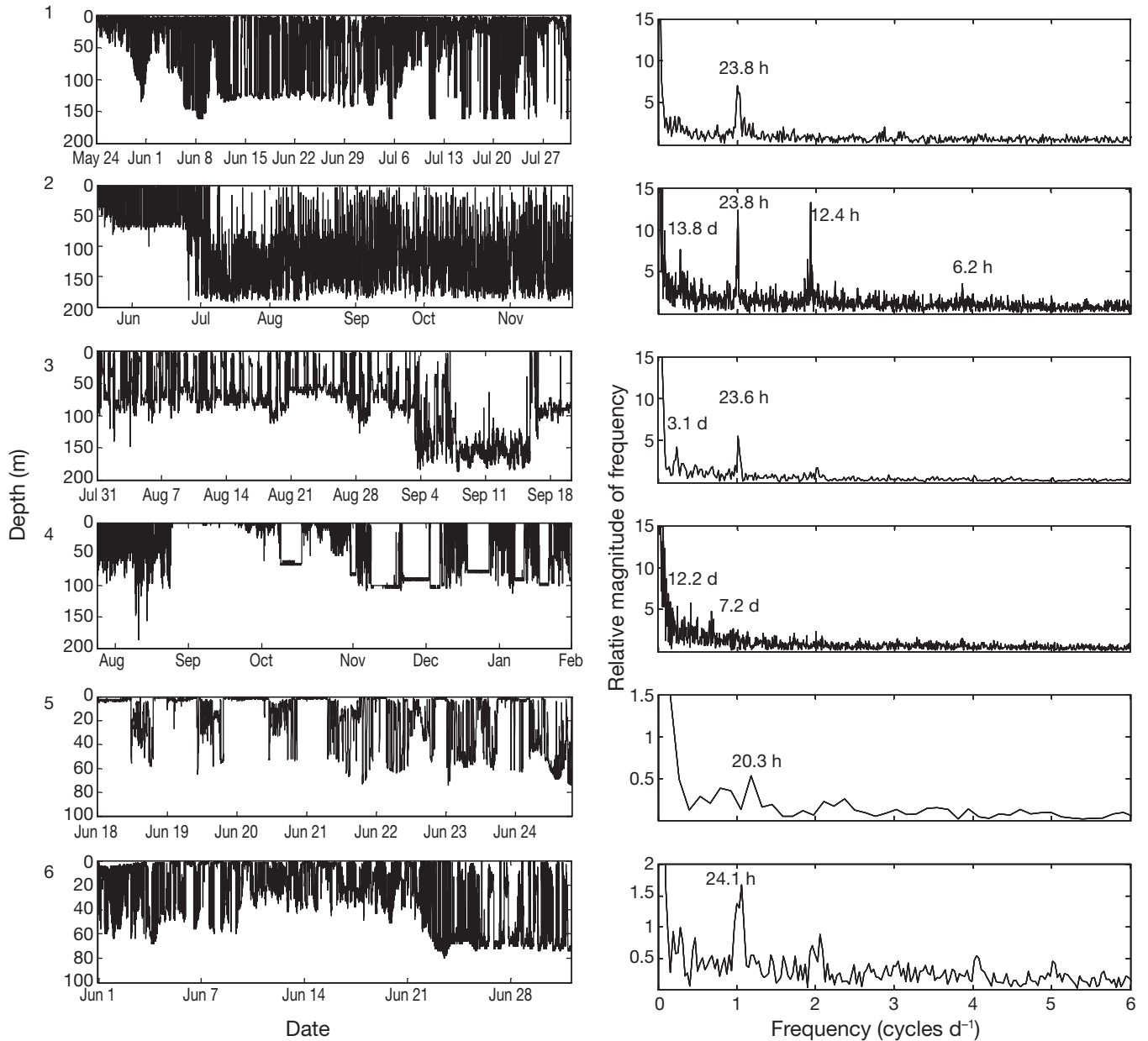


Fig. 1. *Cetorhinus maximus*. Archival records of diving behaviour for 6 basking sharks with the respective FFT-generated periodogram for the raw depth data at 1 min interval resolution. Shark number used in the text is indicated on left. Note tracks differ in duration. The x-axes of the periodograms are truncated at 6 cycles d⁻¹ as there were no spectral peaks that stood above the background noise beyond this domain. Periods of the main spectral peaks found using the raw data and the hamming window are labelled on the periodograms in hours (h) or days (d)

which were harmonics. Harmonics combine to describe the main cyclical component and occur when a behaviour is not exactly sinusoidal in character (Chatfield 1996). The only shark track that did not exhibit a strong overall diel component was that of Shark 4. Visual inspection of the tracks revealed that sharks conducted DVM for 11 to 72% of their individual track time, which collectively accounted for 154 d, or 26% of the total track duration.

Circatidal movements

The strongest spectral peak in the periodogram of shark 2 had a period of 12.35 h, which was not identified in the periodograms for any other shark. The 12.35 h periodicity was out of phase with the diel cycle, but matched the 12.4 h period of the tidal cycle (Fig. 2). There were no geolocations for this shark between July and 6 December; however, its position was geolocated

Table 2. *Cetorhinus maximus*. Summary statistics for the diel pattern of vertical movement (DVM) for each shark during yo-yo dives. Mean rates of ascent and descent are given for yo-yo dives; p-values are also given showing that the rate of descent differs from the ascent within yo-yo dives (Wilcoxon paired-sample tests)

Shark no.	Max. depth	Mean ascent (m min ⁻¹)	Mean descent (m min ⁻¹)	p-value	% time DVM
1	160	0.37	0.48	<0.0005	33
2	192	0.20	0.54	<0.005	24
3	186	0.23	0.40	<0.0005	72
4	186	0.11	0.12	<0.01	11
5	80	0.14	0.24	<0.0005	71
6	174	0.20	0.31	<0.0005	36

by Argos receivers aboard polar-orbiting satellites in Hurd Deep (49.87° N, 2.42° W) when the tag surfaced on 7 December 2001. It is likely, therefore, that the shark remained in this location between July and December, as the combination of depths experienced by the shark and the isothermal water column are not found in any other location on the shelf (Le Fevre 1986).

Shark 2 conducted a tidal pattern of vertical movement almost continuously in the last 2 wk of July (Fig. 2). During this time, the shark's movements had an amplitude of 80 m (from around 90 to 170 ± 10 m; Fig. 2). The shark moved deeper in the water column after local high water and ascended after low water. The shark's descent also coincided with the period of maximal tidal streaming up the channel in an easterly direction, which occurs 36 min following local high water and at speeds of around 1.15 m s⁻¹ (R. D. Pingree pers. comm.). Overall, the shark was significantly shallower on the flood tide than on the ebb (Mann-Whitney *U*-test: median depth on the ebb tide = 160 m, median depth on the flood = 112 m, *W* = 13601002.5, *p* < 0.000, *n* = 4541).

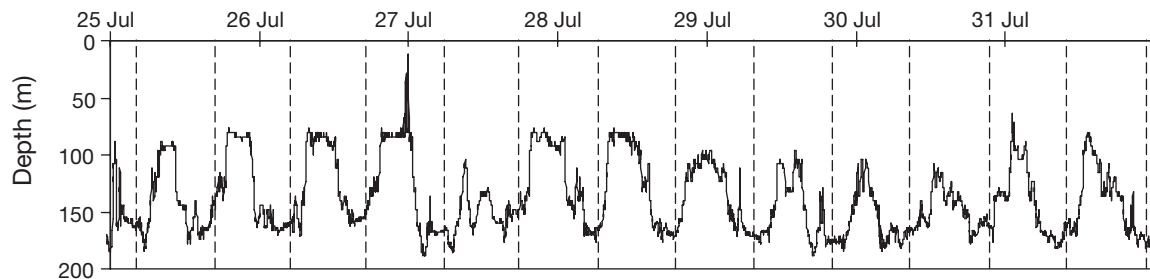


Fig. 2. *Cetorhinus maximus*. Circatidal vertical movement in Shark 2. Times of low water are indicated by dashed vertical lines to demonstrate consistency of the shark's movements with the tidal phase

The periodogram for Shark 2 also had a small spectral peak at 3.89 cycles d⁻¹, or 1 cycle 6.17 h⁻¹, which was exactly double the tidal peak at 1.94 cycles d⁻¹ (Fig. 1). This could be a harmonic, however movements with a corresponding period of 6.17 h were also observable in the track where the shark was deepest at times of high and low water.

Lunar periodicity

The third largest spectral peak in the periodogram for Shark 2 had a period of 13.8 d, which corresponded well with the 14 d spring–neap tidal cycle, and was not present in the periodogram for any other shark. This was confirmed by a significant circular–linear correlation between lunar phase and daily vertical distance moved (*r* = 0.29, *p* < 0.001, *n* = 78 d). The 14 d periodicity was also evident in the pattern of vertical distance moved per day with greater vertical activity during spring tides (Fig. 3).

Seasonal patterns

The strength of all periodic components varied at a monthly scale. Shark 4 represented the longest deploy-

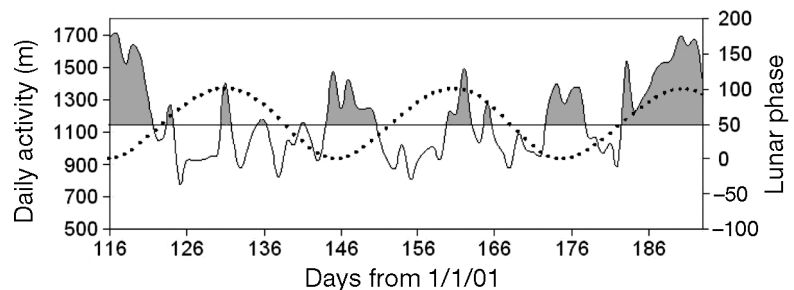


Fig. 3. *Cetorhinus maximus*. Sum of daily vertical activity of basking shark (continuous curve) in relation to lunar phase (dotted curve). Horizontal line denotes mean value of sum of daily vertical activity, with occurrence of activity greater than the mean blocked in grey shade. Peaks in daily activity coincide with spring tides, which occur around 0 and 100% of the lunar phase (peaks and troughs of dotted line)

ment. Monthly periodograms for this shark confirmed an overall lack of periodicity, with small spectral peaks with periods of 1 d in August, 6.94 and 3.86 d in November and 3.97 and 1.46 d in December.

Time spent conducting DVM within any given month varied from 0 to 97%. Monthly periodograms revealed that the diel rhythm was strongest in June and September in Shark 2 (Fig. 4). A similar pattern was observed in the averaged seasonal abundance of copepods in this area, with peaks in June and September (Fig. 5). Whilst data were not available spanning these months for other sharks, all remaining tracks >30 d showed a reduction in diel periodicity in mid-summer in comparison with that observed in the months either side. Shark 1 had a strong diel peak in June but lacked a diel peak in July, Sharks 3 and 4 had diel peaks in August that were not present in September, and September to February respectively.

In Shark 2 the 12.4 h spectral peak first appeared in July, which coincided with a decline in the power of

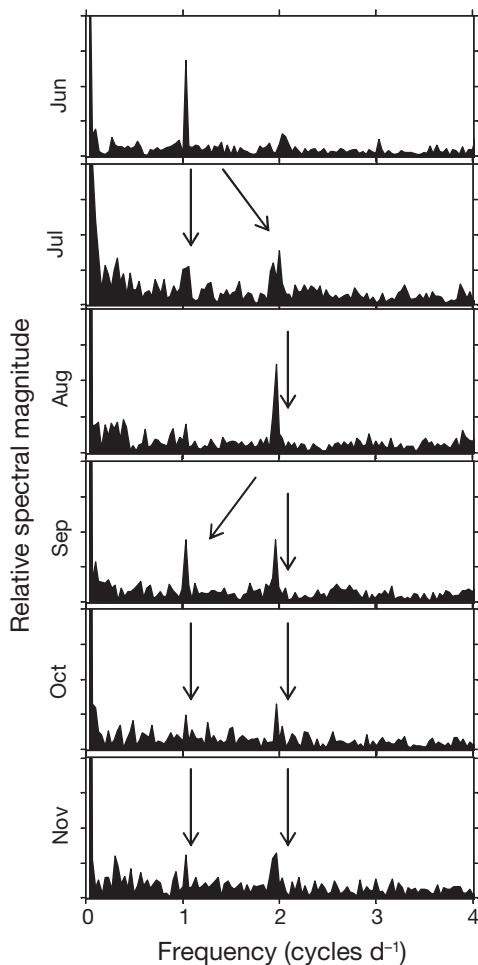


Fig. 4. *Cetorhinus maximus*. Monthly periodograms for Shark 2 showing how strength of the 2 main frequency components fluctuated through time

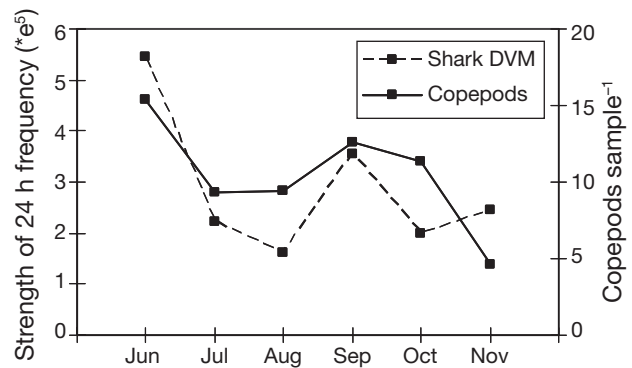


Fig. 5. *Cetorhinus maximus*. Relative strength of diel frequency of vertical movement (DVM) for Shark 2 and monthly abundance of copepods recorded by the CPR survey in an area comprising western English Channel out to the shelf edge

the diel peak. The strong tidal component remained present through to November (Fig. 4) with both diel and tidal rhythms being influential during September. The amplitude of both the diel and tidal periodicities declined from September to November. Visual inspection of the Shark 2 track also revealed a seasonal pattern in yo-yo diving, being present for up to 7 d in May, June and July but absent from August to December.

DISCUSSION

The application of FFTs to vertical movement data from electronic tags is a relatively new development in the field of marine vertebrate behaviour. Fourier methods have been employed to detect periodicity in movement patterns from ultrasonic telemetry (Hartill et al. 2003, Mitamura et al. 2005). However, the direct relationship of the sampling frequency and duration to the resolution of the Fourier output make the FFT well suited to the analysis of archival data. Previous application of these methods to archival data revealed diel and lunar periodicity in the vertical movements of a single whale shark, *Rhincodon typus* (Graham et al. 2006) and confirmed a strong diel rhythm of diving in 10 bigeye tuna *Thunnus obesus* (Musyl et al. 2003). This study is the first to analyse fine-scale vertical movements of multiple individual sharks over seasonal scales using signal processing techniques. The archival tag data, totalling 595 d, included the longest continuous high-resolution diving record for a planktivorous shark (229 d) and the first detailed records of basking shark vertical movements in winter. Whilst factors such as reproduction and temperature are likely to be influential, this study highlighted the importance of prey movements in influencing patterns of vertical activity of *Cetorhinus maximus*.

FFT-generated periodograms for 5 of 6 sharks had a strong spectral peak with a period of 1 cycle d^{-1} representing diel vertical migration (DVM). In 4 tracks (Sharks 1, 3, 5 and 6) this was the strongest frequency component. Vertical movements with a diel pattern have been identified previously in sections of 4 basking shark tracks, where individuals appeared to track both normal and reverse patterns of vertical migration in their zooplankton prey (Sims et al. 2005). However, the prevalence of this behaviour through time was unknown. At a monthly scale the occurrence of both diel migrations appeared to reflect seasonal variations in zooplankton behaviour. The strength of diel periodicity showed a bimodal monthly pattern across sharks, similar to the seasonal abundance of their zooplankton prey on the western European shelf. A bimodal seasonal pattern has also been documented in the zooplankton biomass undertaking daily migrations in the NE Atlantic that was explained largely by seasonal cycles in zooplankton biomass (Hays 1996). Patterns of diving in North Atlantic right whales *Eubalaena glacialis* tracked across 2 consecutive summers have also been correlated with the strength of diel migration in their zooplankton prey (Winn et al. 1995).

Yo-yo diving also varied through time, being observed only during the summer months in Shark 2. Yo-yo diving is likely to represent prey-searching behaviour (Sims et al. 2003). As calanoid copepods such as *Calanus finmarchicus* and *C. helgolandicus* overwinter in deep waters from 100 to 2200 m (Hirche 1983), yo-yo diving in basking sharks may only be appropriate in the summer months (May to September) when the vertical location of their zooplankton prey is more variable. This builds on findings of previous work which showed that basking sharks do not hibernate, but show a seasonal reduction in time spent near the surface, in accordance with the large-scale seasonal movement of their prey away from surface waters (Sims et al. 2003).

Studies of marine predators have frequently identified differences in foraging patterns at different times of year that are often related to associated changes in oceanography, topography or prey species (Green et al. 2005). In this context it is interesting to note that the only change in behaviour from September to December for Shark 2, which appeared to remain in the same location, was a reduction in the strength of periodicity in its vertical movements. This may reflect a reduction in prey availability.

A 12.35 h rhythm was found to be strong in the vertical movements of Shark 2, which corresponded well with the semidiurnal lunar constituent of the tidal cycle (an average of 12.42 h on most coastlines; Queiroga & Blanton 2005). This periodicity represented an active behaviour as the amplitude of the shark's movements (80 m) was far greater than the 4 m range of the M_2

tidal constituent in the area where the shark was tracked (Le Fevre 1986). Circatidal behaviour appeared important, as the 12.35 h spectral peak was larger than that representing DVM, which occurred for 24% of the total track time. A further spectral peak with the same periodicity as the fortnightly spring-neap tidal cycle confirmed the influence of the lunar cycle on this shark. This is the first time, to our knowledge, that tidal patterns of activity have been shown directly in the vertical movements of a pelagic predator from archival tagging data. A lunar influence has been described in other marine predators, which appeared to modulate their diving behaviour in relation to lunar phase (e.g. Horning & Trillmich 1999, Graham et al. 2006). However, it is likely that the basking shark in our study was responding to the amplitude of the tide rather than levels of moonlight as this spectral peak had a period of half the full lunar cycle (28 d).

Tidal rhythms have been documented to influence the horizontal movements of several pelagic predators in coastal areas. Basking sharks have been found to follow the direction of tidal streams for up to 27 h, tracking rich patches of zooplankton aggregated in tidal fronts (Sims & Quayle 1998). Similarly, *Eubalaena glacialis* tracked a patch of *Calanus finmarchicus* as it was horizontally advected by the tide in the lower Bay of Fundy (Baumgartner et al. 2003). Tidal currents can cause particularly high aggregations of prey when they interact with steep topography (Genin 2004). In the St. Laurentian Channel, the flood tide aggregates concentrations of krill and capelin *Mallotus villosus* against a steep slope near the mouth of the estuary (Cotte & Simard 2005). The tidal aggregations are intensified by the negative phototaxis of the krill (Cotte & Simard 2005), which attract large numbers of predators including minke and fin whales *Balaenoptera acutorostrata* and *B. physalus*, respectively (Lavoie et al. 2000).

The circatidal behaviour identified in the present study appeared to be specific to Hurd Deep in the English Channel, as the onset of circatidal movements coincided with the shark's movement into the deep at the beginning of July. The 12.4 h rhythm remained influential in the track over the following 5 mo when the shark remained near the deep. Furthermore, this was the only shark with a full archival record to be located in this area. The duration of this behaviour and the fact that this shark moved into deeper habitat at a time when large numbers of sharks are known to concentrate in surface waters to feed (Sims & Quayle 1998) suggests these tidal movements may be linked to feeding. A tidal pattern of movement may have arisen if the shark tracked zooplankton that actively adjusted their vertical position in response to the tidal cycle. However, this appears unlikely as a tidal pattern of vertical migration has only been documented in plankton asso-

ciated with estuaries, where it is adopted to conduct selective tidal-stream transport to move towards or away from the estuary, or maintain a position in a productive feeding area (Queiroga & Blanton 2005).

Alternatively, tidal streams may accumulate zooplankton found at depth against the topographic relief of Hurd Deep. Populations of *Calanus helgolandicus* and *C. finmarchicus*, the predominant prey of basking sharks, have been found at depth in summer as well as winter months (Hirche 1983). These deep populations usually consist of adults and Copepodid Stage V individuals with large oil sacs (Hirche 1983, Hays et al. 2001), and are therefore likely to be among the most energy-rich sources of prey for basking sharks when found in sufficient concentration. In support of this suggestion, right whales have been observed to bypass vertically migrating *C. finmarchicus* in the summer in order to feed selectively on a deep diapausing layer (Baumgartner et al. 2003).

Furthermore, by analogy with similar studies, physical data is consistent with the possibility that zooplankton may be aggregated by tidal streams in Hurd Deep. The strongest tidal currents on the continental shelf around NW Europe are found near Hurd Deep (Le Fevre 1986). Tidal currents at maximum streaming flow almost exactly in line with the deep, implying that as the flood tide moves in an easterly direction along the deep, it has the potential to concentrate zooplankton at its head. Importantly, the eastern end of the deep is the precise position where the archival tag popped up following release from the shark on 7 December 2001. It is possible that the shark moved down in the water column after maximum flow on the flood tide to exploit zooplankton aggregations as they formed against the sloping sides of the deep. The fortnightly tidal rhythm could have arisen if stronger currents during spring tides aggregated zooplankton in Hurd Deep from a greater volume of water, providing enhanced foraging opportunities and hence greater vertical activity. Likewise, in the St. Laurentian estuary, the fortnightly tidal cycle modulates the intensity with which krill is aggregated against the head of the channel (Lavoie et al. 2000).

The strong influence of DVM in the tracks overall suggests that *Cetorhinus maximus* spend a significant amount of time tracking the vertical movements of their prey. If the strength of the circatidal signal in Shark 2 corresponded to the length of time conducting this behaviour then this shark spent a minimum of 50% of its track time conducting diel and tidal movements. Sharks may also track their prey without marked vertical activity, as the occurrence of DVM in zooplankton varies within and between species, being correlated with variables including body size and condition, pigmentation and ontogeny (Hays 1996, Hays et al. 2001). Both Sharks 3 and 4 displayed periods of ≤ 14 d with lit-

tle vertical activity. The percentage time *C. maximus* spent conducting DVM (11 to 72%) is therefore likely to underestimate the time that these predators track the movements of their prey.

Patterns of vertical movement in Shark 4 differed from those found in the other sharks in almost all respects, from the general character of its vertical movements (Fig. 1) to the similarity in rate of ascent and descent within yo-yo dives (Table 2). It is uncertain why the rate of descent was significantly greater than the rate of ascent in the other sharks, particularly given the variability of this relationship across pelagic planktivores (Cartamil & Lowe 2004, Graham et al. 2006). However, the consistency of this relationship in *C. maximus* may indicate some functionality. Fourier analysis of Shark 4 diving behaviour revealed relatively small spectral peaks that were not identified in any other track. It is uncertain whether these frequencies represented an adaptive behaviour or periodicity in the shark's movements that arose by chance. The length of basking sharks at first maturity is not well established, but it has been suggested to be from 4 to 6.1 m in males (Pauly 2002). At 2.5 m, Shark 4 was a minimum of 2 m shorter than other tagged sharks and, by inference, the only definite juvenile. The distinct vertical movement patterns in Shark 4 may be linked to the foraging inexperience or differing energetic requirements of this individual.

Overall, the FFT can be viewed as a useful tool with which to identify periodicity in vertical movements of marine fishes. Where it identifies a rhythm closely linked to physical processes such as tidal cycles, it also demonstrates the utility of predator movements for providing insight into behavioural and physical mechanisms underlying rhythmic aggregations of their prey. This in turn can identify locations of enhanced productivity that may be of importance to diverse organisms. However, the FFT also has limitations. For instance, visual inspection of Shark 4's dive record revealed a loose pattern of DVM throughout August (~13% of the total track) interspersed with yo-yo dives, but there was no spectral peak at 1 cycle d^{-1} in the periodogram for the track due to the interference of adjacent frequency components. For this reason the FFT may also be less well-suited to the detection of rhythmicity in vertical movement data from air-breathing vertebrates. The strong influence of a diel rhythm in other sharks may also have influenced the ability to detect higher frequency components, which may themselves have been treated as noise. Hence, there is a need to analyse portions of each data series as well as the whole to check that no distinct patterns remain undetected. Finally, the application of Fourier methods yields no information on where signals exist in the time domain at a finescale (Chatfield 1996). Thus, there is a

strong case for using Fourier in conjunction with analysis to identify where periodic influences occur in the archival time series obtained from an animal-attached tag. This temporal dimension may provide interesting insights into when and how marine vertebrates adapt their behaviour to a changing environment.

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